

SIGNIFICANCE OF THE MORPHOLOGICAL CHARACTERS USED IN HIGHER-LEVEL NATURAL CLASSIFICATION OF COLEOPTERAN LARVAE¹

M.G. de Viedma and M.L. Nelson²

ABSTRACT: Significance of the morphological characters used in higher-level natural classification of coleopteran larvae. The three suborders of Coleoptera (Archostemata, Adephaga, and Polyphaga) are differentiated by the larval morphology of the leg, mandible, and hypopharynx and prementum. Regarding the Polyphaga, various schemes have been devised to separate the superfamilies of this largest group. Peyerimhoff (1933) divided the Polyphaga into the Haplogastra and Symphiogastra based upon leg segmentation and urogomphi articulation. The Polyphaga is divided by Van Emden (1942) into three groups on the basis of maxillary lobe development: the first group has a dominant inner lobe (Staphyloidea, Hydrophiloidea, and Scarabaeoidea); the second group possess two well-developed, free maxillary lobes (Dascilloidea and Malacodermata-Sternoxia); and the third group has a dominant outer lobe (Cucujoidea, Betsychoidea, Chrysomeloidea, and Curculinoidea). Crowson's (1967) distillation and improvement of previous works is used to rank characters according to the number of superfamilies of Polyphaga they can separate and, consequently, this method rates the presence or absence of articulated urogomphi as the character of primary importance.

DESCRIPTORS: Coleoptera; Archostemata; Adephaga; Polyphaga; larval characters.

The literature (Boving and Craighead, 1931; Peyerimhoff, 1933; van Emden, 1942; Crowson, 1967; Viedma, 1972) has consistently shown that, at the several levels of a natural classification of coleopteran larvae, various morphological characters display different degrees of importance. As a result, certain characters are repeatedly used to separate the suborders and superfamilies of larvae, while other characters are restricted to the differentiation of lesser taxa. The present paper, recognizing this fact, attempts to describe and determine the relative significance of characters that, through the years, have been used to differentiate the higher taxa.

Several authors (Kolbe, 1908; Forbes, 1926; Boving and Craighead, 1931) have suggested the desirability of adding a third suborder, the Archostemata, to the two long-accepted suborders of Coleoptera, the Adephaga and

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² Contribution No. 351 from the Department of Biology, Wayne State University, Detroit, Michigan 48202, U.S.A.

³ Department of Zoology and Entomology, School of Forestry, Polytechnic University of Madrid, Spain, and Department of Biology, Wayne State University.

Polyphaga. Boving and Craighead's work, which intentionally stresses larval characters, bases its separation of the Archostemata on its possession of an "almost extinct larval type."

The characters used in defining the larvae of the three suborders are shown in Table 1. As noted, the number of leg segments, including the claws, differentiates the Archostemata and the Adephaga from the Polyphaga. Two additional characters, the possible possession of a molar part by the mandibles and the degree of fusion and hardening of the hypopharynx and prementum, separate the Archostemata from the Adephaga. Peyerimhoff (1933) agrees with the formation of the suborder Archostemata, and he splits the Polyphaga into two groups. Within the larval Polyphaga, Peyerimhoff distinguishes between the Haplogastra (with five leg segments and absent or articulated urogomphi) and the Symphiogastra (with five leg segments, or less, or no legs, and with or without urogomphi, but never articulated).

Table 1

	<u>Legs</u>	<u>Mandibles</u>	<u>Hypopharynx and Prementum</u>
Archostemata	Six-segmented with a distinct tarsus and one or two claws	Possessing a strong molar part	Fused into a hard, strong unit
Adephaga	Six-segmented with a distinct tarsal joint and one or two movable claws	Lacking a molar part	Never united into a hard, strong unit
Polyphaga	Five-segmented; tarsal joint fused with a single claw into a tarsungulus; or less than five-jointed; or no legs present		

Van Emden (1942), in his discussion of British beetle larvae, separates the Adephaga and the Polyphaga, the two suborders he lists, on the number of leg segments. He notes that the Adephaga have the tarsus and tibia separate and possess six-segmented legs and, generally, two claws (not considered a segment). The Polyphaga, in contrast, have the tarsus and tibia fused and, if legs are present, possess ones with five or less segments and only one claw. He further divides the Polyphaga into three groups on the basis of maxillary lobe development. The first group, consisting of the superfamilies Staphyloidea,

Hydrophiloidea, and Scarabaeoidea, has a dominant inner lobe (i.e., mouthparts of Caraboid facies). In the second group, composed of the superfamily Dascilloidea and the Malacodermata-Sternoxia, are found two well-developed, free maxillary lobes. The last group, containing the Cucujoidea, Bostrychoidea, Chrusomeloidea and Curculinoidea, has a dominant outer lobe. Viedma (1972) agrees that the two characters used by van Emden, viz., leg segmentation and maxillary lobe development, are of primary importance at this taxonomic level.

A fourth suborder, Myxophaga, is suggested for the Coleoptera by Crowson (1967). Although he states that the larvae of the Myxophaga are "not yet satisfactorily characterizable," he finds in them some characters common to the Polyphaga. Based on his system, among the principal characters that divide the suborders is the presence (in the Adepfaga and the Archostemata) or the absence (in the Myxophaga and the Polyphaga) of a distinct tarsus and claw. He also uses the sclerome of the hypopharynx: the Adepfaga having a hypopharynx without sclerome; the Arcostemata a hypopharynx with a "characteristic heavy, dark sclerome;" and the Myxophaga and Polyphaga "without such a heavy sclerome." The Adepfaga is further removed from the other suborders in having a labrum fused with the head capsule (that is, not free) and, as noted by Boving and Craighead, lacking a mandibular molar part (mola).

Among the repeatedly used, therefore, significant, characters for the differentiation of larvae in the suborders of Coleoptera are the legs (i.e., number of leg segments present) and, to a lesser extent, the mouthparts (the sclerome of the hypopharynx, the mandibular mola, and the maxillary lobes).

The relative significance of series-level characters is not considered here because the positions of the several series are not, at this time, generally accepted by coleopterists.

The study of characters differentiating the superfamilies of Polyphaga, which are the classic higher-level taxa, is facilitated by observing the characters used for separation in a so-called "natural key." Crowson's work (1967) has been chosen for this purpose because it is a distillation and improvement of previous keys. Obviously, the earlier a character appears in the key, the more important it is, involving, as it does, more groups in the key. In this respect, therefore, it is possible to assign to the characters a classificatory "weight" and, on that basis, a rank that corresponds with the number of superfamilies each differentiates (Table 2). Naturally, characters used to separate the same number of superfamilies, that is, having the same "weight", have an equal rank. Only the characters that are actually compared in the dichotomous key (i.e., those contained in both parts of a couplet) are

used. Lesser characters stated in only one portion of a couplet are not comparable, and cannot be included. Additionally, if the several mandibular and maxillary characters are combined, these two encompassing characters will naturally achieve a higher classificatory weight, rank, and significance than will any of the characters from which they were derived. For that reason, the mouthpart characters are used specifically in superfamily determination, and, consequently, are kept separate in this discussion.

This procedure shows that the character of primary significance is the presence or absence of articulated urogomphi. This character separates the Scarabaeoidea, Hydrophiloidea, Staphyloidea, and Histeroidea from other superfamilies lacking this character. Table 2 and the diagram that follows reflect this statement. It should be noted that the Scarabaeoidea lack articulated urogomphi (which is later stated in the key). This does not necessarily mean that the Scarabaeoidea belong to the Symphiogastra. In fact, according to Crowson (1970), the larvae of the Scarabaeoidea seem related to the Dascilloidea, while the adults seem related to the Haplogastra. He concludes that the relationship of the Scarabaeoidea to either of the above seems mutually exclusive. Therefore, inclusion of the Scarabaeoidea into the group possessing articulated urogomphi represents one of the few weak points in the key. The second most important character is the presence or absence of a distinct maxillary galea and lacinia. This character is used to differentiate three superfamilies of the Haplogastra and fourteen of the Symphiogastra. The third most important set of characters, and ones ranked equally, are the presence of long bristles on the tenth abdominal segment and, when legs are present, the lack of a trochanter. These characters diagnose the Stylopoidea and differentiate them from other superfamilies in the Symphiogastra. It should be noted here that the appearance of the Stylopoidea at this point in the key cannot be considered natural. This superfamily, with its strikingly different larvae, was once considered an order. Its position is not clear. Crowson later (1970) puts it in the Cucujiformia.

Another way of examining the significance of coleopteran larval characters at the superfamily level is shown by Diagram 1. In this representation of character-superfamily relationship, the cumulative number of superfamilies differentiated by a particular character is taken, as before, as indicative of relative importance. It demonstrates that the primary character (presence or absence of articulated urogomphi) separates all superfamilies of Polyphaga into two groups. Following this dichotomy, the character ranked second in importance (presence or absence of distinct galea and lacinia) is used to differentiate three superfamilies of the Haplogastra and fourteen of the Symphiogastra. In this manner the relative value of any character and its

relationships to various superfamilies can be determined at once. It can be seen that some characters appear in the diagram more than once. This situation is caused by its use within different "branches" of the key (for example, character no. 2 in the Haplogastra and Symphiogastra), or its use (for example, in character no. 6) in conjunction with other characters at different points within the same "branch."

In summary, it appears to us that the taxonomic significance of different morphological characters varies with the level of the taxa being discussed. The most significant classificatory character used for the determination of the suborders in the larvae of Coleoptera is the degree of leg segmentation. The most important differentiating character at the superfamilial level, with respect to Polyphaga, is the presence or absence of articulated urogomphi. In a broader sense, therefore, it can be seen that, through the process of analyzing a key, it is possible to give scale and definition to the over-used and imprecise concept of "taxonomic importance." This process yields a hierarchy of characters according to the relative size of their spheres of influence (i.e., their actual taxonomic importance) and also indicates, at any given level, the most efficient method of utilizing characters.

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Table 2

Character Number	"Weight"	Rank	Character
1	19	1	with or without (w/wo) articulated urogomphi
2	17	2	maxillae w/wo distinct galea and lacinia
3	15	3	10 th abdominal segment w/wo long bristles
4	15	3	w/wo trochanters when legs present
5	14	4	w/wo corneous urogomphi
6	14	4	maxillae w/wo well-developed articulating area
7	14	4	mandibles w/wo mola
8	14	4	w/wo labrum free
9	10	5	w/wo well-developed legs (usually more than 2 segments)
10	7	6	maxillae w/wo distinct galea and spur-like lacinia
11	7	6	9 th abdominal tergite w/wo distinct urogomphi
12	7	6	w/wo cribriform spiracles
13	7	6	w/wo finger-like galea
14	6	7	w/wo spiracles closed and tracheal gills present
15	6	7	mandibles w/wo distinct prostheca
16	5	8	w/wo mouth-parts possibly protracted
17	5	8	w/wo long epicranial suture
18	2	9	maxillae w/wo galea born on elongate palpiger
19	2	9	mandibles w/wo perforation or channelling along inner margins
20	2	9	general form cylindrical OR flattened
21	2	9	w/wo body soft and C-shaped
22	2	9	head w/wo distinct gula
23	2	9	w/wo tergal sclerites
24	2	9	w/wo prothorax enlarged
25	2	9	maxillary mala entire OR partially divided at apex
26	2	9	labium w/wo sclerotised transverse hypopharyngeal bar
27	2	9	antennae well-developed (3 segments) OR reduced (1 or 2 segments)

Diagram 1: Distribution of Larval Characters (using character numbers from Table 2).

Superfamilies

